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Morphological variation in skull shape and size across extinct and extant populations of the greater stick-nest rat (*Leporillus conditor*): implications for translocation
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1 **Title:** Morphological variation in skull shape and size across extinct and extant populations
2 of the greater stick-nest rat (*Leporillus conditor*): implications for translocation

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12
13 **Running Head:** Morphological variation of *Leporillus conditor*

14
15 **Table of Contents Summary:** Local variation in size and shape can have implications for
16 individuals' abilities to persist in different habitats. We measured historical specimens of a
17 frequently translocated species, the greater stick-nest rat, and found that significantly larger
18 body size in arid and island populations, but no overall shape variation. This absence of local
19 adaptation in shape suggests that the island population, which is the last remaining extant
20 population of the species, is likely suitable for mainland translocations.

21
22 **Abstract**

23
24 Within-species morphological variation is often observed across spatial and climatic
25 gradients. Understanding this variation is important to conservation planning, as specialised
26 adaptations may influence a population's persistence following translocation. However,
27 knowing whether local adaptations are prevalent within a species can be challenging when
28 the species has undergone range contractions. Here, we used museum specimens to study size
29 and shape variation of the greater stick-nest rat (*Leporillus conditor*). We aimed to determine
30 whether intraspecific size and shape variation previously existed within the species across its
31 historical range, and inform on possible implications for translocations of the remaining
32 extant population. We found significantly larger skull size in the Franklin Islands and arid

33 populations, possibly indicating a historically continuous population experiencing similar
34 selection pressures such as high predation pressure, competition with other large arid zone
35 rodents or climatic extremes. Conversely, skull shape variation within the species adheres to
36 an allometric trajectory, indicating no specific local adaptations of skull shape. This absence
37 of local skull shape adaptation suggests that the Franklin Islands population is likely suitable
38 for mainland translocations. However, further research into the historical phylogeography of
39 the species is recommended to identify whether large size resulted from shared ancestry or
40 convergent evolution.

41

42 **Additional Keywords**

43

44 Conserved cranial allometry, morphology, rodent, reintroduction biology

45

46 **Introduction**

47

48 Intraspecific morphological variation can vary spatially due to phenotypic plasticity, natural
49 selection and adaptation, or genetic drift (Price et al. 2003; de Abreu et al. 2018). This
50 variation may be a response to spatial or temporal variation in climate, competition, predation
51 pressure, habitat or diet (Alexander et al. 2006; Campbell-Tennant et al. 2015; Foth et al.
52 2015; Lostrom et al. 2015; Onley et al. 2020). Many Australian taxa exhibit morphological
53 variation across their range in response to various ecological and environmental changes
54 (Keast 1968; Lostrom et al. 2015); the Lakeland Downs mouse (*Leggadina lakedownensis*),
55 for example, presents considerable morphological variation across its range, including island
56 gigantism (Cooper et al. 2003). However, anthropogenic range contractions, extirpations and
57 habitat fragmentation, are known to reduce intraspecific morphological diversity and
58 population structure (e.g. Thomson *et al.*, 2018).

59

60 Understanding intraspecific variation in morphology is relevant to threatened species
61 conservation for several reasons. Firstly, much of conservation biology is species-orientated
62 and descriptions of geographic variation in morphology are important for delineating
63 biological species and resolving taxonomic issues (Dubois 2003; Godfray et al. 2004). For
64 example, morphological studies of intraspecific variation in Australian bandicoots (genus
65 *Perameles* and *Chaeropus*) has recently resulted in the identification of a number of new
66 species from within what was traditionally thought to be a single species (Travouillon and

67 Phillips 2018; Travouillon et al. 2019). At a finer scale, knowledge of intraspecific
68 morphological variation can complement population genetic data to identify geographic
69 population structure and intraspecific units for conservation (Arnoux et al. 2014; Hounkpèvi
70 et al. 2020). Further, knowledge of morphological variation is critical when planning
71 translocations that involve two or more source populations. Mixing phenotypically different
72 populations may prevent or reduce interbreeding if pre-zygotic isolation exists (Alexandrino
73 et al. 2005; Latch et al. 2006), which can produce offspring that are maladapted to the local
74 environment, or can lead to non-random mating between source populations (Charlesworth
75 and Willis 2009; Thavornkanlapachai et al. 2019). Finally, morphological studies can be used
76 to quantify how within species diversity has changed following a bottleneck (Lovatt 2007).

77
78 Identifying the extent of morphological variation within species is a necessary, but often
79 overlooked component in planning reintroductions and translocations. Local adaptations or
80 plasticity in fragmented populations may be a key element for survival and persistence.
81 Although difficult to determine from morphology alone, knowledge of whether physical
82 variation is due to natural selection or phenotypic plasticity is critical to identify whether a
83 population could adapt to a new environment or selective pressure *in situ* or following
84 translocation (Lema and Nevitt 2006; Ficetola et al. 2016). Variation due to phenotypic
85 plasticity may produce favourable results and improve the rate of population establishment
86 (Haddaway et al. 2012); for example, a mainland translocation of an island population of
87 golden bandicoot (*Isodon auratus*) resulted in an increase in fecundity, skeletal size and
88 body mass within four generations, which researchers suggested was a result of a reduction in
89 competitive pressures (Dunlop and Morris 2018). Local adaptations, however, may result in
90 reduced fitness following translocation if they not suited to the translocation site (Hereford
91 2009; Taylor et al. 2021). For example, Taylor et al. (2021) suggested that Shark Bay
92 bandicoots (*Perameles bougainville*) translocated to the arid zone of Australia may not
93 possess the necessary auditory adaptations for predator avoidance in a desert environment.
94 Further, sock-eye salmon (*Oncorhynchus nerka*) adapted to a beach environment
95 demonstrated reduced reproductive success when colonising a stream environment (Peterson
96 et al. 2014). This reduction in fecundity was attributed to limitations resulting from the
97 beach-adapted salmon's larger body size, which made them more susceptible to predation
98 and stranding, and limited their access to mates and spawning sites in shallower areas.

99

100 Rodents are exemplary for exhibiting morphological variation across wide geographical
101 ranges and a variety of environmental conditions (Maestri et al. 2016; Assis et al. 2017). For
102 example, species in arid habitats have larger bullae in order to detect low frequency sounds
103 and longer nasal passages to aid respiratory water retention (Lay 1972; Alhajeri and Stepan
104 2018; Basso et al. 2020). These adaptations can result from factors such as changes in food
105 availability, rainfall, primary productivity, or thermoregulatory requirements under varying
106 climates, and can lead to functional differences between populations (Walsh et al. 2016).
107 Therefore, when developing translocation strategies, conservationists should not assume that
108 all populations will respond homogeneously to different environments across the species'
109 distribution, particularly if the reintroduction site is markedly different from the source
110 (Zaidaneen and Hasaseen 2008). However, despite being universally recognised as critical to
111 survival (Schlichting 1986; Agrawal 2001), local morphological adaptation is rarely
112 considered during translocation planning and assessment. This is of particular concern for
113 species that historically had wide geographical ranges and many potential ecotypes (Mee et
114 al. 2015) but have declined to a single habitat type or restricted areas. One such species is the
115 greater stick-nest rat (*Leporillus conditor*), an endemic Australian rodent that has been the
116 subject of multiple translocations since the 1980s. Although *L. conditor* has suffered a
117 considerable range contraction in the past two centuries (Copley 1999), the species once
118 inhabited a large geographical range encompassing many habitat types and bioregions, from
119 mesic coastal environments to the arid zone. However, its rapid population decline has
120 resulted in limited knowledge of the species' historic morphological variation, including
121 potential adaptations to environmental variation such as maximum/minimum temperature,
122 shelter sites and food and water availability. Increased mortality has also been noted in
123 reintroduced *L. conditor* at an arid site during periods of extreme heat stress (Bolton and
124 Moseby 2004), despite the site being encompassed by the species' historical range. This
125 raises concerns for the heat tolerance thresholds of this population, having been sourced from
126 the southernmost, and most mesic, point of the species' range and translocated to the arid
127 zone.

128

129 In this study, we use morphometric analyses of museum specimens to identify patterns of
130 morphological variation in skull shape and size across the species' former range. We aim to
131 determine whether intraspecific variation existed across the historic distribution of *L.*
132 *conditor* as a result of adaptations to environmental niches, and inform on possible
133 implications for the conservation management of the species. Given that populations isolated

134 on islands often display divergent phenotypes in comparison to their mainland counterparts
135 (e.g. island gigantism/dwarfism) (Case 1978), it is expected that the single extant population
136 of *L. conditor* will differ in size (and associated allometric shape variation) compared with
137 the extinct mainland populations. Further, given the variety of habitat types encompassed
138 (e.g., desert, plains), some morphological diversity is expected among the mainland
139 populations in response to environmental gradients such as climate and vegetation.

140

141 **Methods**

142

143 *Study Species*

144 Following European arrival and the introduction of feral predators and herbivores, as well as
145 land use changes, *L. conditor* was extirpated from its entire mainland Australian range, with
146 just a single population surviving on the Franklin Islands, off the coast of Ceduna, South
147 Australia by the early 1900s (Copley 1999). This population was briefly classified as a
148 separate species, *L. jonesi*, but has since been synonymised with *L. conditor* (Copley, 1999;
149 Thomas, 1921). What little is known about the historical range of this murid rodent has been
150 gathered from subfossils, nest remains, sightings by early naturalists, and voucher specimens
151 in natural history collections (Copley 1999). In the mid-1980's, after an extensive ecological
152 study of the Franklin Island populations, a captive breeding program began and was shortly
153 followed by multiple translocation efforts to Reevesby and St Peters Islands, as well as
154 several fenced reserves (Van Dyck et al. 2008; Short et al. 2019). While some reintroduction
155 efforts have been successful, such as those at Salutation Island and the Arid Recovery
156 Reserve, others, including translocations to reserves at Venus Bay and Faure Island, failed
157 due to predation by species such as feral cats and raptors (Woinarski and Burbidge 2016;
158 Short et al. 2019).

159

160 *Samples*

161 A total of 199 partial and whole skulls (preserved as skeletal material) of *Leporillus conditor*
162 from 34 locations across the species' historic range were sourced from the Mammal and
163 Palaeontology collections at the South Australian Museum, Adelaide (SAM), the Western
164 Australian Museum, Perth (WAM) and Museum Victoria, Melbourne (MV) (Table 2,
165 Supplementary Table 1). In addition, morphometric data recorded in Tate (1951) of the type
166 specimen of *L. jonesi* and of a *L. conditor* specimen collected at Ooldea, South Australia by
167 E. Troughton were included. To assess environmental variation across the geographic range

168 of *L. conditor*, individuals were grouped according to the Interim Biogeographic
169 Regionalisation for Australia (IBRA) classification system (Table 2, Figure 2). IBRA regions
170 are a classification system that separate Australia's landscapes into 89 geographically distinct
171 bioregions characterised by common vegetation, habitat, geology and climate (Thackway and
172 Cresswell 1995; Environment Australia 2000).

173

174 *Cranial and Dental Measurements*

175 Fifteen linear measurements of the cranium and mandible (Figure 1, Table 1) were taken
176 using iGaging Absolute Origin digital calipers developed from common linear
177 morphometrics used in past studies of rodents, including features associated with climatic
178 variation such as rostra length and width (Musser and Piik 1982; Voss 1988; Mortelliti et al.
179 2012; Fabre et al. 2013; Alhajeri and Steppan 2018). Although bullae were measured during
180 data collection as a point of interest of adaptation to aridity, these features were not available
181 for the majority (86%) of the samples, and were therefore excluded from the final analysis.
182 Cranial material was chosen for this study over skins, as shrinkage of skins can distort
183 physical features and may confound morphological studies (Horie 1990; Shu et al. 2017).
184 Where one side of the mandible was available, measurements were taken from that side;
185 where both were available, a side was chosen at random. Where only part of the skull was
186 available, measurements were only recorded for features that were not broken or damaged.
187 Specimen age was determined by examining the tooth wear of the individual, as well as the
188 ossification of the cranial plates and of the suture between the basioccipital and basisphenoid
189 bones (Gustafson and Malmö 1950; Morris 1972; Pankakoski 1980). In cases where a
190 specimen was identified as juvenile, no cranial measurements were taken. With the exception
191 of the Tate and Troughton specimens, all measurements were taken by one researcher (I.R.O)
192 to minimise observer error. As a measure of repeatability, a subset of measurements was used
193 to determine the intraclass correlation coefficient (ICC) using the R package "ICC" (version
194 2.3.0).

195

196 *Data Analysis*

197 All analyses were completed using the R Statistical Environment (version 4.0.2) (R Core
198 Team 2021). Due to the poor condition of some of the cranial material 53% of the
199 measurements were missing from the full dataset. In order to maximise the sample size
200 among localities, missing values were imputed using the *mice* function in R package "mice"
201 (version 3.12.0), that creates multiple imputations for missing data based on fully conditional

202 specification (Buuren and Groothuis-Oudshoorn 2011; Clavel et al. 2014). This method was
203 chosen over single imputation procedures, as it takes into account the uncertainty of missing
204 value estimation (Zhang 2016). The model was trained on existing measurements in the
205 dataset, that then informed the imputation of the missing data over 100 iterations.

206

207 Skull size and shape were treated separately for analysis, but the relationship between the two
208 (allometry) was also examined (Mosimann, 1970). Skull size was calculated as the geometric
209 mean of all variables in the imputed dataset, and taken to be a proxy for body size
210 (Mosimann 1970; Meachen-Samuels and Van Valkenburgh 2009). This allowed for a
211 conservative estimate of size without confounding by shape variation in individual
212 measurements, but was supported by tests using three other common indicators of body size,
213 greatest length of the skull (GLS) and upper and lower molar tooth row length (MTR/mTR)
214 (Millien and Bovy 2010; Freudenthal and Martín-Suárez 2013; Bertrand et al. 2015). Skull
215 shape was calculated using the log-shape ratio approach to standardise for isometric scaling
216 differences, where the imputed linear variables were divided by the skull size of all variables
217 and log-transformed (Mosimann and James 1979).

218

219 To determine if there were differences in skull size between rats sampled from different
220 IBRA regions, the skull size of individuals in each region were compared using a non-
221 parametric one-way analysis of variance (ANOVA; Kruskal-Wallis test), followed by a
222 pairwise Wilcoxon rank sum test to identify which groups were significantly different,
223 implemented in the R package “stats” (version 4.1.0). This approach was used as the data was
224 not normally distributed, even when a log transformation was applied. Box plots were used to
225 visualise cranial size variation within and among regions.

226

227 To determine if there were differences in skull shape among IBRA regions, a non-parametric
228 ANOVA for multivariate data was implemented using the *procD.lm* function in the R
229 package “geomorph” (version 3.3.2). Here the model included log-transformed skull size as a
230 covariate to calculate the proportion of variance in the dataset that was due to allometry (the
231 size term), while the proportion due to regional differences was provided by the size:region
232 interaction term. To ensure that the imputation method was consistent and reliable, a loop
233 was created that completed 100 iterations of the above process, and the mean and standard
234 deviations of the coefficient of determination (R^2) and P-values were inspected. For graphical
235 representation of the results, a multivariate regression analysis was applied to visualise the

236 allometric shape variation, using the regression score approach (Drake & Klingenberg 2008),
237 and a principal components analysis of the regression residuals was performed to visualise
238 the non-allometric shape variation among IBRA regions.

239

240 Finally, to test whether morphological variation was correlated with environmental variables,
241 we ran linear regressions between morphological measurements and two key climate
242 variables (mean annual temperature and mean annual precipitation), as well as latitude and
243 longitude. Climate data was extracted from the Atlas of Living Australia's Spatial Portal
244 using the following layers: CSIRO Ecosystem Sciences mean annual temperature (°C) and
245 mean annual rainfall (mm).

246

247 **Results**

248

249 Of the 201 individuals in the dataset, 13 had no missing data, 26 had 1-25% missing data, 64
250 had 26-50% missing data, and 98 had more than 50% missing data. Across all samples there
251 was a total of 53% missing data. Multiple imputation has been found to remain unbiased to
252 ~50% missingness, and so this proportion of missing data was considered acceptable
253 (Marshall et al. 2010; Lee and Carlin 2012; Haji-Maghsoudi et al. 2013). Following ICC
254 analysis of a subset of measurements to determine repeatability, the ICC value was
255 determined to be >0.9, indicating excellent reliability of measurements (Wolak 2015; Koo
256 and Li 2016).

257

258 *Skull size and shape variation*

259 IBRA regions accounted for 40% (mean $R^2 = 0.3976$) of size variation (Table 3, Part A)
260 among all individuals (P-value <0.001). Pairwise comparisons using the Wilcoxon rank sum
261 test revealed that the individuals that differ most from all others were those from the Eyre
262 Yorke Block and Simpson Strzelecki Dunefields (although they were not significantly
263 different from each other) (Supplementary Information 2). Skulls from individuals from these
264 two regions were the largest in the dataset (Figure 2). Tests using the standard size-proxy
265 linear variables GLS, MTR and mTR corroborated this pattern (Supplementary Information
266 3).

267

268 For skull shape, size accounted for 14% (mean $R^2 = 0.1411$; Table 3, Part B) and IBRA
269 regions accounted for 21% (mean $R^2 = 0.2107$; Table 3, Part C) of the variation among

270 individuals (both P-value <0.001). Samples followed a global allometric trajectory (Figure
271 3A), and while some regional groups were separated along this trajectory there was clear
272 overlap of groups spanning the size distribution. Only 4% (mean $R^2 = 0.041$) of shape
273 variation was due to regional size differences, and these differences were not statistically
274 significant (mean P-value 0.1333) (Table 3, Part D). No differences among groups were
275 found in the skull shape regression residuals (Figure 3B). This indicates that there is skull
276 shape variation between regional groups, but this is mostly due to allometric differences
277 corresponding to the observed size variation (Figure 2) and not specific local adaptation
278 acting on skull shape. No individual areas of the skull emerged as having noticeable shape
279 variation across the IBRA regions, and so further study into individual linear variables was
280 not deemed necessary. Individuals from the Eyre Yorke Block and Simpson Strzelecki
281 Dunefields clustered at the larger end of the spectrum, indicating a larger skull size and
282 inferred body size.

283

284 *Spatial and climatic correlations*

285

286 Given that skull size emerged as the dominant morphological trait varying among IBRA
287 regions, we tested for spatial and climatic correlations in skull size variables only. Significant
288 positive correlations were apparent between skull size and annual mean precipitation (P-value
289 = 0.0042), latitude (degrees south) (P-value <0.001) and longitude (P-value <0.001). There
290 was a significant negative correlation between skull size and annual mean temperature (P-
291 value <0.001). However, all but one model had considerable outliers, as evidenced by their
292 low R^2 values (Figure 4). Longitude produced the best fit, with an R^2 value of 0.25. *L.*
293 *conditor* individuals increased in size as longitude increased (i.e., from west to east).

294

295

296

297 **Discussion**

298

299 Morphometric analysis of *L. conditor* skull size and shape revealed considerable size
300 differences between sampled locations and predictable shape variation across its historical
301 distribution. Allometric shape (the component proportional to size) dominated the variation
302 among individuals of *L. conditor*, indicating that apparent skull diversity is due to body size
303 differences and does not suggest local adaptation acting on skull shape. This is a common
304 observation in Australian rodents; a study by Marcy *et al.* (2020) of 38 Australian rodent

305 species found low variation in skull shape across all taxa, with size explaining the majority of
306 the variation. The authors suggested that this universal skull shape is an evolutionary
307 adaptation dating back over ten million years and is the secret to rodents' success in a variety
308 of habitats. It is therefore unsurprising that little shape variation is present in historical
309 populations of *L. conditor*, despite the variety of environmental conditions the species
310 encompassed.

311
312 Skull size, a proxy for body size, varied significantly across the historical range. Our analyses
313 indicate that individuals from the Eyre Yorke Block IBRA region (containing the Franklin
314 Islands and a population translocated to Reevesby Island from the Franklins) and individuals
315 from the Simpson Strzelecki Dunefields are significantly larger than all other sampled
316 locations. While our models using climate variables did not reveal a clear correlation with
317 skull size, there are several possible ecological explanations for these observations. As no
318 other major herbivores inhabit the Franklin Islands (Copley 1999), the observed size increase
319 in individuals belonging to the Franklin Island populations may be due to predation pressure
320 from black tiger snakes (*Notechis ater niger*) and barn owls (*Tyto alba*) that regularly prey on
321 juvenile *L. conditor* (and likely smaller adults) (Robinson 1975; Read 1984; Copley 1988,
322 1999). The equally large size of individuals from central arid Australia (Simpson-Strzelecki
323 Dunefields) (all of which were collected in close proximity to the Lake Eyre Basin but were
324 not collected following a flood year) may be due to similar predation pressures from desert
325 reptiles such as snakes and goannas (Bolton and Moseby, 2004). Indeed, the similarity in size
326 between these populations of *L. conditor* and their geographical proximity suggest that these
327 larger individuals may once have belonged to a continuous population that became separated
328 by rising sea levels ~8,000 years ago (Robinson et al. 1996). Genetic analysis of historical
329 specimens would further inform on this possibility.

330
331 An alternative explanation for the large body size of the arid *L. conditor* may be character
332 displacement, or ecological release, intensified by limited resources in a desert environment
333 (Brown and Wilson 1956; Grant 1972; Strong et al. 1979; Herrmann et al. 2021). Species that
334 are closely related and of similar size often compete more intensely than those of disparate
335 size (Larsen 1986; Violle et al. 2011). Increased competition with other rodents such as the
336 long-haired rat (*Rattus villosissimus*) in the arid zone may therefore have resulted in the
337 evolution of larger body size in the northern population of *L. conditor*, in order to expand its
338 niche and access alternative resources in a competitive environment (Bowers and Brown

339 1982; Bolnick et al. 2010). Another alternative selection pressure that should be considered is
340 that smaller animals can be more sensitive to extreme temperatures as they have a larger
341 surface area to volume ratio and a narrower thermal neutral zone, meaning that
342 thermoregulatory costs are lower for larger animals when temperatures are highly variable
343 (Grodzinski and Weiner 1984; Degen et al. 1997). As daily temperature ranges of 15°C -
344 20°C are typical in the Australian desert (Trewin 2006), climate extremes may have acted as
345 a selection pressure for larger body size in *L. conditor*. Support for this comes from a study of
346 fat sand rats (*Psammomys obesus*), where under extreme ambient temperatures body mass of
347 adults correlated positively with time spent foraging, suggesting that larger size allows for
348 better thermoregulation in a desert environment (Haim et al. 2006).

349

350 Individuals from the easternmost region, the Darling Riverine Plains, straddled the margin
351 between the two apparent size morphotypes in the dataset. Although not significantly larger
352 than the other mainland populations, individuals in this region were not significantly smaller
353 than the larger morphotypes, either. This pattern may be consistent with a west-east size
354 gradient. Indeed, of our climate and spatial correlation analyses, longitude was found to be
355 the variable of best fit to skull size. There are several examples of east-west variation in other
356 Australian taxa, such as the Hooded Plover, (Weston et al. 2020); however, in many cases
357 genetic studies have determined this variation to represent multiple species, with the
358 Nullarbor Plain acting as a driver of speciation (Rix et al. 2015). Evidence of east-west
359 vicariance has been observed in many taxa, including phascogales (Spencer et al. 2001),
360 pygmy perch (Buckley et al. 2018), aquatic beetles (Hawlitshchek et al. 2011), and eucalypts
361 (Ladiges et al. 2010). The individual from the Riverina, however, did not adhere to this
362 pattern, but with a sample size of one we cannot make sound inferences for this region.
363 Indeed, our small sample size and sparse spatial distribution overall prevents any robust
364 conclusions here, but molecular phylogeographic studies would provide further insight.

365

366 *Limitations*

367 Due to the incomplete preservation of many of the skulls used in this study, our dataset had a
368 high degree of missing values (53%). Although imputations using the “mice” R package
369 produced consistent results, the uncertainty associated with this amount of missing data must
370 be acknowledged as a caveat. Another limitation that must be considered is the small sample
371 size and patchy representation across *L. conditor*'s former range. As the species became
372 extinct on the mainland almost a century ago, very little material is available that

373 characterises its historic distribution. Here we have attempted to obtain a representative
374 sample of the variety of habitat types and environmental conditions experienced by the
375 species, but acknowledge that the sample sizes are not equal between regions, and there
376 remains much that we do not know about *L. conditor*'s former life history.

377

378 *Implications for translocation*

379 *Leporillus conditor* has been used in several translocation programs in recent decades, with
380 the Franklin Islands population acting as the primary source (Pedler and Copley 1993; Short
381 et al. 2018, 2019; White et al. 2018). Our analyses show that these individuals are likely
382 larger than their extinct counterparts in most mainland locations, with the exception of central
383 Australia. Whether this morphological variation has an impact on fitness when translocating
384 Franklin Island individuals to other areas of Australia is difficult to determine, as the
385 relationship between form and function is highly complex and context-dependent (Koehl
386 1996). Small morphological changes may have considerable consequences for some species,
387 such as Darwin's finches (Grant and Grant 2002; Herrel et al. 2005), while in other cases
388 phenotypic variation has no influence on performance (Warner and Shine 2006).

389

390 Encouragingly, however, the lack of non-allometric shape variation in *L. conditor* among
391 regions indicates that the species likely conforms to the universally well-adapted cranial form
392 observed in many Australian rodent species, and may be capable of simply scaling its body
393 size when necessary to adapt to an ecological niche (Marcy et al. 2020). Further studies on
394 body size changes over time in relation to community composition in translocated *L. conditor*
395 populations would provide more clarity here. In addition, genetic analysis of historic
396 populations of *L. conditor* would provide insight as to genetic spatial variation and
397 phylogeography within the species prior to its mainland extinction, as well as determining
398 whether the large size of some *L. conditor* populations is the result of phenotypic plasticity or
399 variation in genetic structure. Morphological studies of species that have undergone
400 significant declines and range contractions are encouraged prior to conducting
401 reintroductions, as this information may assist with population establishment.

402

403 **Data Availability Statement**

404

405 Data used to generate these results is contained in the supplementary information and is
406 available at the University of Adelaide FigShare (<https://doi.org/10.25909/18319349>).

407

408 **Conflicts of Interest**

409

410 The authors declare no conflicts of interest.

411

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413

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430 **References**

- 431
- 432 Agrawal, A. A., 2001. Phenotypic Plasticity in the Interactions and Evolution of Species.
 433 Science, 294 (5541), 321–326.
- 434 Alexander, H. J., Taylor, J. S., Wu, S. S.-T. and Breden, F., 2006. Parallel evolution and
 435 vicariance in the guppy (*Poecilia reticulata*) over multiple spatial and temporal
 436 scales. *Evolution; International Journal of Organic Evolution*, 60 (11), 2352–2369.
- 437 Alexandrino, J., Baird, S. J. E., Lawson, L., Macey, J. R., Moritz, C. and Wake, D. B., 2005.
 438 Strong selection against hybrids at a hybrid zone in the *Ensatina* ring species complex
 439 and its evolutionary implications. *Evolution; International Journal of Organic*
 440 *Evolution*, 59 (6), 1334–1347.
- 441 Alhajeri, B. H. and Stepan, S. J., 2018. A phylogenetic test of adaptation to deserts and
 442 aridity in skull and dental morphology across rodents. *Journal of Mammalogy*, 99 (5),
 443 1197–1216.
- 444 Arnoux, E., Eraud, C., Navarro, N., Tougard, C., Thomas, A., Cavallo, F., Vetter, N., Faivre,
 445 B. and Garnier, S., 2014. Morphology and genetics reveal an intriguing pattern of
 446 differentiation at a very small geographic scale in a bird species, the forest thrush
 447 *Turdus lherminieri*. *Heredity*, 113 (6), 514–525.
- 448 Assis, A. P. A., Rossoni, D. M., Patton, J. L. and Marroig, G., 2017. Evolutionary processes
 449 and its environmental correlates in the cranial morphology of western chipmunks
 450 (*Tamias*). *Evolution*, 71 (3), 595–609.
- 451 Basso, A. P., Sidorkewicz, N. S., Casanave, E. B. and Mason, M. J., 2020. The middle ear of
 452 the pink fairy armadillo *Chlamyphorus truncatus* (*Xenarthra*, *Cingulata*,
 453 *Chlamyphoridae*): comparison with armadillo relatives using computed tomography.
 454 *Journal of Anatomy*, 236 (5), 809–826.
- 455 Bertrand, O., Schillaci, M. and Silcox, M., 2015. Cranial dimensions as estimators of body
 456 mass and locomotor habits in extant and fossil rodents. *Journal of Vertebrate*
 457 *Paleontology*, 36, 1–10.
- 458 Bolnick, D. I., Ingram, T., Stutz, W. E., Snowberg, L. K., Lau, O. L. and Paull, J. S., 2010.
 459 Ecological release from interspecific competition leads to decoupled changes in
 460 population and individual niche width. *Proceedings of the Royal Society B:*
 461 *Biological Sciences*, 277 (1689), 1789–1797.
- 462 Bolton, J. and Moseby, K., 2004. The activity of Sand Goannas *Varanus gouldii* and their
 463 interaction with reintroduced Greater Stick-nest Rats *Leporillus conditor*. *Pacific*
 464 *Conservation Biology*, 10 (3), 193.
- 465 Bowers, M. A. and Brown, J. H., 1982. Body Size and Coexistence in Desert Rodents:
 466 Chance or Community Structure?: *Ecological Archives E063-002*. *Ecology*, 63 (2),
 467 391–400.
- 468 Brown, W. and Wilson, E., 1956. Character displacement. *Systematic zoology*, 5 (2), 49–64.
- 469 Buckley, S. J., Domingos, F. M., Attard, C. R., Brauer, C. J., Sandoval-Castillo, J., Lodge, R.,
 470 Unmack, P. J. and Beheregaray, L. B., 2018. Phylogenomic history of enigmatic
 471 pygmy perches: implications for biogeography, taxonomy and conservation. *Royal*
 472 *Society open science*, 5 (6), 172125.
- 473 Buuren, S. van and Groothuis-Oudshoorn, K., 2011. mice: Multivariate Imputation by
 474 Chained Equations in R. *Journal of Statistical Software*, 45 (1), 1–67.
- 475 Campbell-Tennant, D. J. E., Gardner, J. L., Kearney, M. R. and Symonds, M. R. E., 2015.
 476 Climate-related spatial and temporal variation in bill morphology over the past
 477 century in Australian parrots. *Journal of Biogeography*, 42 (6), 1163–1175.
- 478 Case, T. J., 1978. A General Explanation for Insular Body Size Trends in Terrestrial
 479 Vertebrates. *Ecology*, 59 (1), 1–18.

- 480 Charlesworth, D. and Willis, J. H., 2009. The genetics of inbreeding depression. *Nature*
481 *Reviews Genetics*, 10 (11), 783–796.
- 482 Clavel, J., Merceron, G. and Escarguel, G., 2014. Missing Data Estimation in
483 *Morphometrics: How Much is Too Much?* *Systematic biology*, 63, 203–218.
- 484 Cooper, N. K., Adams, M., Anthony, C. and Schmitt, L., 2003. Morphological and genetic
485 variation in *Leggadina* (Thomas, 1910) with special reference to Western Australian
486 populations. *Records of the Western Australian Museum*, 21, 333–351.
- 487 Copley, P., 1999. Natural histories of Australia’s stick-nest rats, genus *Leporillus* (*Rodentia* :
488 *Muridae*). *Wildlife Research*, 26 (4), 513.
- 489 Copley, P. B., 1988. The stick-nest rats of Australia : a final report to World Wildlife Fund
490 (Australia). National Parks and Wildlife Service, Dept. of Environment and Planning.
491 Adelaide, South Australia
- 492 de Abreu, F. H. T., Schietti, J. and Anciães, M., 2018. Spatial and environmental correlates of
493 intraspecific morphological variation in three species of passerine birds from the
494 Purus–Madeira interfluvium, Central Amazonia. *Evolutionary Ecology*, 32 (2), 191–
495 214.
- 496 Degen, A. A., Khokhlova, I. S., Kam, M. and Nagy, K. A., 1997. Body size, granivory and
497 seasonal dietary shifts in desert gerbilline rodents. *Functional Ecology*, 11 (1), 53–59.
- 498 Dubois, A., 2003. The relationships between taxonomy and conservation biology
499 in the century of extinctions. *Comptes Rendus Biologies*, 326, 9–21.
- 500 Dunlop, J. and Morris, K., 2018. Environmental determination of body size in mammals:
501 Rethinking ‘island dwarfism’ in the golden bandicoot. *Austral Ecology*, 43 (7), 817–
502 827.
- 503 Environment Australia, 2000. Revision of the Interim Biogeographic Regionalisation of
504 Australia (IBRA) and the Development of Version 5.1 - Summary Report. Canberra,
505 Australia: Department of Environment and Heritage.
- 506 Fabre, P.-H., Pagès, M., Musser, G. G., Fitriana, Y. S., Fjeldså, J., Jennings, A., Jönsson, K.
507 A., Kennedy, J., Michaux, J., Semiadi, G., Supriatna, N. and Helgen, K. M., 2013. A
508 new genus of rodent from Wallacea (*Rodentia: Muridae: Murinae: Rattini*), and its
509 implication for biogeography and Indo-Pacific Rattini systematics. *Zoological Journal*
510 *of the Linnean Society*, 169 (2), 408–447.
- 511 Ficetola, G. F., Colleoni, E., Renaud, J., Scali, S., Padoa-Schioppa, E. and Thuiller, W., 2016.
512 Morphological variation in salamanders and their potential response to climate
513 change. *Global change biology*, 22 (6), 2013–2024.
- 514 Foth, C., Bona, P. and Desojo, J. B., 2015. Intraspecific variation in the skull morphology of
515 the black caiman *Melanosuchus niger* (*Alligatoridae, Caimaninae*). *Acta Zoologica*,
516 96 (1), 1–13.
- 517 Freudenthal, M. and Martín-Suárez, E., 2013. Estimating body mass of fossil rodents, 130.
- 518 Godfray, H. C. J., Knapp, S. and Mace, G. M., 2004. The role of taxonomy in species
519 conservation. *Philosophical Transactions of the Royal Society of London. Series B:*
520 *Biological Sciences*, 359 (1444), 711–719.
- 521 Grant, P. R., 1972. Convergent and divergent character displacement. *Biological Journal of*
522 *the Linnean Society*, 4 (1), 39–68.
- 523 Grant, P. R. and Grant, B. R., 2002. Adaptive radiation of Darwin’s finches: Recent data help
524 explain how this famous group of Galapagos birds evolved, although gaps in our
525 understanding remain. *American Scientist*, 90 (2), 130–139.
- 526 Grodzinski, W. and Weiner, J., 1984. Energetics of small and large mammals. *Acta*
527 *Zoologica Fennica*, 172, 7–10.
- 528 Gustafson, G. and Malmö, D. O., 1950. Age Determinations on Teeth. *The Journal of the*
529 *American Dental Association*, 41 (1), 45–54.

- 530 Haddaway, N. R., Mortimer, R. J. G., Christmas, M., Grahame, J. W. and Dunn, A. M., 2012.
531 Morphological diversity and phenotypic plasticity in the threatened British white-
532 clawed crayfish (*Austropotamobius pallipes*). *Aquatic Conservation: Marine and*
533 *Freshwater Ecosystems*, 22 (2), 220–231.
- 534 Haim, A., Alma, A. and Neuman, A., 2006. Body mass is a thermoregulatory adaptation of
535 diurnal rodents to the desert environment. *Second International Meeting on*
536 *Physiology and Pharmacology of Temperature Regulation*, 31 (1), 168–171.
- 537 Haji-Maghsoudi, S., Haghdoost, A.-A., Rastegari, A. and Baneshi, M. R., 2013. Influence of
538 Pattern of Missing Data on Performance of Imputation Methods: An Example from
539 National Data on Drug Injection in Prisons. *International Journal of Health Policy and*
540 *Management*, 1 (1), 69–77.
- 541 Hawlitschek, O., Porch, N., Hendrich, L. and Balke, M., 2011. Ecological niche modelling
542 and nDNA sequencing support a new, morphologically cryptic beetle species unveiled
543 by DNA barcoding. *PLoS One*, 6 (2), e16662.
- 544 Hereford, J., 2009. A Quantitative Survey of Local Adaptation and Fitness Trade-Offs. *The*
545 *American Naturalist*, 173 (5), 579–588.
- 546 Herrel, A., Podos, J., Huber, S. K. and Hendry, A. P., 2005. Evolution of bite force in
547 Darwin's finches: a key role for head width. *Journal of Evolutionary Biology*, 18 (3),
548 669–675.
- 549 Herrmann, N. C., Stroud, J. T. and Losos, J. B., 2021. The Evolution of 'Ecological Release'
550 into the 21st Century. *Trends in Ecology & Evolution*, 36 (3), 206–215.
- 551 Horie, C., 1990. Deterioration of skin in museum collections. *Polymer Degradation and*
552 *Stability*, 29 (1), 109–133.
- 553 Hounkpèvi, A., Salako, V. K., Donhouédé, J. C. F., Daï, E. H., Tovissodé, F., Kakai, R. G.
554 and Assogbadjo, A. E., 2020. Natural intraspecific trait variation patterns of the wild
555 soursop *Annona senegalensis* (*Annonaceae*) along a climatic gradient in Benin, West
556 Africa. *Plant Ecology and Evolution*, 153 (3), 455–465.
- 557 Keast, A., 1968. Competitive Interactions and the Evolution of Ecological Niches as
558 Illustrated by the Australian Honeyeater Genus *Meliphreptus* (*meliphagidae*).
559 *Evolution*, 22 (4), 762–784.
- 560 Koehl, M. A. R., 1996. When does morphology matter? *Annual Review of Ecology and*
561 *Systematics*, 27 (1), 501–542.
- 562 Koo, T. K. and Li, M. Y., 2016. A Guideline of Selecting and Reporting Intraclass
563 Correlation Coefficients for Reliability Research. *Journal of Chiropractic Medicine*,
564 15 (2), 155–163.
- 565 Ladiges, P. Y., Bayly, M. J., Nelson, G. J., Williams, D. M. and Knapp, S., 2010. East-west
566 continental vicariance in Eucalyptus subgenus Eucalyptus. In: *Beyond cladistics: the*
567 *branching of a paradigm*. Berkeley, California: The Regents of the University of
568 California, 267–302.
- 569 Larsen, E., 1986. Competitive release in microhabitat use among coexisting desert rodents: a
570 natural experiment. *Oecologia*, 69 (2), 231–237.
- 571 Latch, E. K., Harveson, L. A., King, J. S., Hobson, M. D. and Rhodes Jr, O. E., 2006.
572 Assessing Hybridization in Wildlife Populations Using Molecular Markers: A Case
573 Study in Wild Turkeys. *The Journal of Wildlife Management*, 70 (2), 485–492.
- 574 Lay, D. M., 1972. The anatomy, physiology, functional significance and evolution of
575 specialized hearing organs of gerbilline rodents. *Journal of Morphology*, 138 (1), 41–
576 120.
- 577 Lee, K. J. and Carlin, J. B., 2012. Recovery of information from multiple imputation: a
578 simulation study. *Emerging Themes in Epidemiology*, 9 (1), 3.

- 579 Lema, S. C. and Nevitt, G. A., 2006. Testing an ecophysiological mechanism of
580 morphological plasticity in pupfish and its relevance to conservation efforts for
581 endangered Devils Hole pupfish. *Journal of Experimental Biology*, 209 (18), 3499–
582 3509.
- 583 Lostrom, S., Evans, J. P., Grierson, P. F., Collin, S. P., Davies, P. M. and Kelley, J. L., 2015.
584 Linking stream ecology with morphological variability in a native freshwater fish
585 from semi-arid Australia. *Ecology and Evolution*, 5 (16), 3272–3287.
- 586 Lovatt, F. M., 2007. A study of the impact of population bottlenecks on the genetics and
587 morphology of reindeer (*Rangifer tarandus tarandus*) on the island of South Georgia.
588 Doctoral. Durham University. Available from: <http://etheses.dur.ac.uk/2315/>
589 [Accessed 18 Mar 2021].
- 590 Maestri, R., Fornel, R., Gonçalves, G. L., Geise, L., Freitas, T. R. O. de and Carnaval, A. C.,
591 2016. Predictors of intraspecific morphological variability in a tropical hotspot:
592 comparing the influence of random and non-random factors. *Journal of*
593 *Biogeography*, 43 (11), 2160–2172.
- 594 Marcy, A. E., Guillerme, T., Sherratt, E., Rowe, K. C., Phillips, M. J. and Weisbecker, V.,
595 2020. Australian Rodents Reveal Conserved Cranial Evolutionary Allometry across
596 10 Million Years of Murid Evolution. *The American Naturalist*, 196 (6), 755–768.
- 597 Marshall, A., Altman, D. G., Royston, P. and Holder, R. L., 2010. Comparison of techniques
598 for handling missing covariate data within prognostic modelling studies: a simulation
599 study. *BMC Medical Research Methodology*, 10 (1), 1–16.
- 600 Meachen-Samuels, J. and Van Valkenburgh, B., 2009. Craniodental indicators of prey size
601 preference in the *Felidae*. *Biological Journal of the Linnean Society*, 96 (4), 784–799.
- 602 Mee, J. A., Bernatchez, L., Reist, J. D., Rogers, S. M. and Taylor, E. B., 2015. Identifying
603 designatable units for intraspecific conservation prioritization: a hierarchical approach
604 applied to the lake whitefish species complex (*Coregonus* spp.). *Evolutionary*
605 *Applications*, 8 (5), 423–441.
- 606 Millien, V. and Bovy, H., 2010. When Teeth and Bones Disagree: Body Mass Estimation of a
607 Giant Extinct Rodent. *Journal of Mammalogy*, 91, 11–18.
- 608 Morris, P., 1972. A review of mammalian age determination methods. *Mammal Review*. 2
609 (3), 69-104
- 610 Mortelliti, A., Castiglia, R., Amori, G., Maryanto, I. and Musser, G. G., 2012. A new species
611 of *Margaretamys* (*Rodentia: Muridae: Murinae: Rattini*) from Pegunungan
612 Mekongga, southeastern Sulawesi, Indonesia. *Tropical Zoology*, 25 (2), 74–107.
- 613 Mosimann, J. E., 1970. Size allometry: size and shape variables with characterizations of the
614 lognormal and generalized gamma distributions. *Journal of the American Statistical*
615 *Association*, 65 (330), 930–945.
- 616 Mosimann, J. E. and James, F. C., 1979. New statistical methods for allometry with
617 application to Florida red-winged blackbirds. *Evolution; International Journal of*
618 *Organic Evolution*, 33 (1Part2), 444–459.
- 619 Musser, G. G. and Piik, E., 1982. A new species of *Hydromys* (*Muridae*) from western New
620 Guinea (Irian Jaya). *Zoologische Mededelingen*, 56, 153–166.
- 621 Onley, I. R., Gardner, J. L. and Symonds, M. R. E., 2020. Spatial and temporal variation in
622 morphology in Australian whistlers and shrike-thrushes: is climate change causing
623 larger appendages? *Biological Journal of the Linnean Society*, 130 (1), 101–113.
- 624 Pankakoski, E., 1980. An improved method for age determination in the muskrat, *Ondatra*
625 *zibethica* (L.). *Annales Zoologici Fennici*, 17 (2), 113–121.
- 626 Pedler, L. and Copley, P., 1993. Re-introduction of stick-nest rats to Reevesby Island, South
627 Australia. South Australian Department of Environment and Land Management:
628 Biological Conservation Branch. Adelaide, South Australia

- 629 Peterson, D. A., Hilborn, R. and Hauser, L., 2014. Local adaptation limits lifetime
630 reproductive success of dispersers in a wild salmon metapopulation. *Nature*
631 *Communications*, 5 (1), 3696.
- 632 Price, T. D., Qvarnström, A. and Irwin, D. E., 2003. The role of phenotypic plasticity in
633 driving genetic evolution. *Proceedings of the Royal Society of London. Series B:*
634 *Biological Sciences*, 270 (1523), 1433–1440.
- 635 R Core Team, 2021. *R: A Language and Environment for Statistical Computing*. Vienna,
636 Austria: R Foundation for Statistical Computing. Available from: [https://www.R-](https://www.R-project.org/)
637 [project.org/](https://www.R-project.org/).
- 638 Read, V. T., 1984. *The Stick-nest Rats of Australia: a preliminary report*. Adelaide: South
639 Australian National Parks and Wildlife Service, Department of Environment and
640 Planning.
- 641 Rix, M. G., Edwards, D. L., Byrne, M., Harvey, M. S., Joseph, L. and Roberts, J. D., 2015.
642 Biogeography and speciation of terrestrial fauna in the south-western Australian
643 biodiversity hotspot. *Biological Reviews*, 90 (3), 762–793.
- 644 Robinson, A. C., 1975. The Sticknest Rat, *Leporillus conditor*, on Franklin Island, Nuyts
645 Archipelago, South Australia. *Australian Mammalogy*, 1 (4), 319–327.
- 646 Robinson, A., Canty, P., Mooney, T. and Rudduck, P., 1996. *South Australia's Offshore*
647 *Islands*. Australian Government Publishing Service, Canberra, New South Wales
- 648 Schlichting, C. D., 1986. The evolution of phenotypic plasticity in plants. *Annual Review of*
649 *Ecology and Systematics*, 17 (1), 667–693.
- 650 Short, J., Copley, P., Ruykys, L., Morris, K., Read, J. and Moseby, K., 2019. Review of
651 translocations of the greater stick-nest rat (*Leporillus conditor*): lessons learnt to
652 facilitate ongoing recovery. *Wildlife Research*, 46 (6), 455.
- 653 Short, J., Richards, J. D. and O'Neill, S., 2018. Reintroduction of the greater stick-nest rat
654 (*Leporillus conditor*) to Heirisson Prong, Shark Bay: an unsuccessful attempt to
655 establish a mainland population. *Australian Mammalogy*, 40 (2), 269.
- 656 Shu, G., Gong, Y., Xie, F., Wu, N. C. and Li, C., 2017. Effects of long-term preservation on
657 amphibian body conditions: implications for historical morphological research. *PeerJ*,
658 5, e3805.
- 659 Spencer, P. B. S., Rhind, S. G. and Eldridge, M. D. B., 2001. Phylogeographic structure
660 within *Phascogale* (*Marsupialia*: *Dasyuridae*) based on partial cytochrome b
661 sequence. *Australian Journal of Zoology*, 49 (4), 369.
- 662 Strong, D. R., Szyska, L. A. and Simberloff, D. S., 1979. Test of community-wide character
663 displacement against null hypotheses. *Evolution*, 897–913.
- 664 Tate, G. H. H., 1951. Results of the Archbold Expeditions. No. 65. The rodents of Australia
665 and New Guinea. *Bulletin of the American Museum of Natural History*, 97, 183–430.
- 666 Taylor, M. C., Travouillon, K. J., Andrew, M. E., Fleming, P. A. and Warburton, N. M.,
667 2021. Keeping an ear out: size relationship of the tympanic bullae and pinnae in
668 bandicoots and bilbies (*Marsupialia*: *Peramelemorphia*). *Current Zoology*.
- 669 Thackway, R. and Cresswell, I. D., 1995. *An interim biogeographic regionalisation for*
670 *Australia: a framework for setting priorities in the National Reserves System*
671 *Cooperative Program*. Canberra: Australian Nature Conservation Agency, Reserve
672 Systems Unit.
- 673 Thavornkanlapachai, R., Mills, H. R., Ottewell, K., Dunlop, J., Sims, C., Morris, K.,
674 Donaldson, F. and Kennington, W. J., 2019. Mixing Genetically and Morphologically
675 Distinct Populations in Translocations: Asymmetrical Introgression in A Newly
676 Established Population of the Boodie (*Bettongia lesueur*). *Genes*, 10 (9), 729.

- 677 Travouillon, K. J. and Phillips, M. J., 2018. Total evidence analysis of the phylogenetic
678 relationships of bandicoots and bilbies (*Marsupialia: Peramelemorphia*):
679 reassessment of two species and description of a new species. *Zootaxa*, 4378 (2), 224.
- 680 Travouillon, K. J., Simões, B. F., Miguez, R. P., Brace, S., Brewer, B., Stemmer, D., Price,
681 G. J., Cramb, J. and Louys, L., 2019. Hidden in plain sight: reassessment of the pig-
682 footed bandicoot, *Chaeropus ecaudatus* (*Peramelemorphia, Chaeropodidae*), with a
683 description of a new species from Central Australia, and use of the fossil record to
684 trace its past distribution. *Zootaxa*, 4566 (1), 1-69.
- 685 Trewin, D., 2006. Year Book Australia. Canberra, Australia: Australian Bureau of Statistics.
- 686 Van Dyck, S., Strahan, R., Museum, Q., Van Dyck, S. and Strahan, R., 2008. The mammals
687 of Australia. New Holland Publishers, Sydney, Australia.
- 688 Violle, C., Nemergut, D. R., Pu, Z. and Jiang, L., 2011. Phylogenetic limiting similarity and
689 competitive exclusion. *Ecology Letters*, 14 (8), 782–787.
- 690 Voss, R. S., 1988. Systematics and Ecology of the ichthyomyine rodents (*Muroidea*): patterns
691 of morphological evolution in a small adaptive radiation. *Bulletin of the American*
692 *Museum of Natural History*, 188, 259–493.
- 693 Walsh, R. E., Assis, A. P. A., Patton, J. L., Marroig, G., Dawson, T. E. and Lacey, E. A.,
694 2016. Morphological and dietary responses of chipmunks to a century of climate
695 change. *Global Change Biology*, 22 (9), 3233–3252.
- 696 Warner, Daniel. and Shine, R., 2006. Morphological variation does not influence locomotor
697 performance within a cohort of hatchling lizards (*Amphibolurus muricatus*,
698 *Agamidae*). *Oikos*, 114 (1), 126–134.
- 699 Weston, M. A., Clarke, K., Maguire, G. S. and Sumner, J., 2020. Morphological and
700 molecular evidence of population divergence in a widespread shorebird across its
701 southern mainland Australian distribution. *Conservation Genetics*, 21 (4), 757–770.
- 702 White, L. C., Moseby, K. E., Thomson, V. A., Donnellan, S. C. and Austin, J. J., 2018. Long-
703 term genetic consequences of mammal reintroductions into an Australian
704 conservation reserve. *Biological Conservation*, 219, 1–11.
- 705 Woinarski, J. C. Z. and Burbidge, A. A., 2016. *Leporillus conditor*. The IUCN Red List of
706 Threatened Species. IUCN Red List of Threatened Species.
- 707 Wolak, M. E., 2015. ICC: Facilitating Estimation of the Intra-class Correlation Coefficient.
708 Available from: <http://github.com/matthewwolak/ICC>.
- 709 Zaidaneen, J. A. and Hasaseen, A. A. A., 2008. Re-introduction of Arabian oryx into Wadi
710 Rum Protected Area, Jordan. In: *Global re-introduction perspectives: Re-introduction*
711 *case studies from around the globe*. Abu Dhabi: IUCN/SSC Re-introduction Specialist
712 Group and Environment Agency Abu Dhabi, 181–184.
- 713 Zhang, Z., 2016. Multiple imputation with multivariate imputation by chained equation
714 (MICE) package. *Annals of translational medicine*, 4 (2), 30–30.

717 **Tables**

718

719 **Table 1** Definitions of abbreviations of the measurements depicted in Figure 1

Abbreviation	Measurement
GLS	Greatest length of skull
CBL	Condylar-basal length
PPM	Parietal to pre-maxillary length
ZB	Zygomatic breadth
IZL	Internal zygomatic length
BB	Breadth of braincase
HB	Height of braincase
IB	Interorbital breadth
RB	Breadth of rostrum
RL	Length of rostrum (nasal bone)
LIF	Length of incisive foramina
BIF	Breadth of incisive foramina
MTR	Maxillary tooth row length
mTR	Mandibular tooth row length
MH	Mandibular height

720

721

722 **Table 2** Sample sizes of *Leporillus conditor* skulls collected in each IBRA region.

IBRA Region	<i>n</i>
Carnarvon	13
Yalgoo	44
Murchison	1
Coolgardie	11
Hampton	12
Nullarbor	70
Eyre Yorke Block	30
Stony Plains	1
Simpson Strzelecki Dunefields	5
Flinders Lofty Block	10
Riverina	1
Darling Riverine Plains	3

723

724

725 **Table 3** Analysis of variance model results for *Leporillus conditor* skull size (log-
 726 transformed geometric mean) against IBRA region, and skull shape (log-shape ratios) against
 727 size and region. Test statistics (F), coefficients of determination (R^2) and P-values are
 728 provided with standard deviations from the 100 iterations of "mice" missing data imputation.

729

A) Size vs IBRA region			
	F	R²	P-value
Mean (±SD)	11.40(±1.3289)	0.3976(±0.0283)	0.001(±0)
Min	8.321	0.3263	0.001
Median	11.360	0.3980	0.001
Max	14.580	0.4590	0.001
B) Shape vs Size			
	F	R²	P-value
Mean (±SD)	37.20(±3.9172)	0.1411(±0.0129)	0.001(±0)
Min	27.15	0.1108	0.001
Median	37.46	0.1409	0.001
Max	46.08	0.1723	0.001
C) Shape vs IBRA region			
	F	R²	P-value
Mean (±SD)	4.592(±0.2907)	0.2107(±0.0105)	0.001(±0)
Min	3.963	0.1874	0.001
Median	4.559	0.2097	0.001
Max	5.483	0.2419	0.001
D) Shape vs Size:IBRA region			
	F	R²	P-value
Mean (±SD)	1.3495(±0.2282)	0.0410(±0.0066)	0.1333(±0.1286)
Min	0.8037	0.0251	0.0030

Median	1.3273	0.0401	0.0975
Max	2.4139	0.0722	0.8120

730

731

732

733 **Figure Legends**

734

735 **Figure 1** Morphological measurements of *Leporillus conditor* cranial material (Image
736 redrawn from Watts and Aslin, 1981). Abbreviations follow in Table 1.

737

738 **Figure 2** Skull size (geometric mean of linear variables) of *Leporillus conditor* per IBRA
739 region, corresponding to a map of collection locations across the historic range of the species
740 (represented by grey hashed area). Size of points on the map reflect the size of individuals
741 from that location. Dotted horizontal line indicates overall mean skull size. See also Table 3,
742 Part A.

743

744 **Figure 3** A) Multivariate regression analysis of *Leporillus conditor* skull size (log-
745 transformed geometric mean) against skull shape and B) the first two axes of a principal
746 components analysis of the regression residuals. Size accounts for 14% (mean $R^2 = 0.1411$)
747 of the shape variation (see Table 3, Part A). Points represent individuals, coloured by IBRA
748 region, and 95% confidence ellipses for each region are drawn in B.

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750

751 **Figure 4** Linear regression analysis of *Leporillus conditor* skull size (log-transformed
752 geometric mean) against climate and spatial variables. Points represent individuals and are
753 coloured by IBRA region. Note that latitude is displayed as degrees south rather than
754 negative values.

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